WHAT CAN BIRDS TELL US ABOUT THE MIGRATION PHYSIOLOGY OF BATS?

Liam P. McGuire* and Christopher G. Guglielmo

Department of Biology, University of Western Ontario, London, Ontario N6A 5B7, Canada (LPM, CGG)

Many species of bats undergo annual migrations, in some cases covering distances of 1,000 km or more. However, very little is known about the physiological and biochemical mechanisms underlying bat migration. In contrast, the physiology of migrating birds has been studied for decades and many migration-related changes have been documented. Although bats and birds evolved flight and long-distance migration independently, they have likely experienced many similar selective pressures. We therefore suggest that knowledge of bird migration physiology can be used to generate predictions for emerging studies of bat migration physiology. In this review, we discuss major physiological and biochemical adaptations relating to fuel acquisition and fuel utilization. For each, we summarize knowledge gained from migration studies of birds and bats (if any) and make predictions of bat migration physiology. For many aspects, we predict that bats will have evolved similar physiological mechanisms to birds. However, there are some potentially major differences in the energetic models for bats and birds, including torpor, fuel selection at high-intensity exercise, and trade-offs between reproduction and migration.

Key words: bats, birds, fuel acquisition, fuel utilization, lipids, migration, nutrient stores, physiology

Our knowledge of bat migration was 1st reviewed nearly 40 years ago by Griffin (1970), and since that time, it is startling how few new data have been published. Recently, interest in all aspects of bat migration has surged, partly due to improvements in tracking techniques (Cryan et al. 2004; Wikelski et al. 2007), but also by the high mortality rates of migrant bats at wind energy facilities (Baerwald and Barclay 2009; Barclay et al. 2007; Cryan and Brown 2007; Cryan and Barclay 2009; Kunz et al. 2007). It is also important that we understand bat migration so that we may assess the impacts of climate change, as already observed in other migratory taxa (e.g., Both and Visser 2001; Cotton 2003).

Migration physiology examines the mechanisms that enable organisms to successfully complete migratory movements. The literature on migration physiology of bats is sparse, whereas birds have been studied intensively for many decades in this context (e.g., Berthold 1993; Gwinner 1990; McWilliams et al. 2004; and many others). Although bats and birds are taxonomically distant, both groups are endothermic vertebrates capable of flight and consequently should be subject to similar selective pressures on their physiology as it relates to flight and migration. For example, similar to birds,

and unlike typical nonvolant mammals, bats have high rates of passive nutrient absorption in the intestine, which is thought to be a mass-reducing adaptation to minimize the cost of flight (Caviedes-Vidal et al. 2007, 2008). In this review, we focus on several key aspects of migration physiology of birds and address how they may apply to bat migration. We limit our discussion to fuel metabolism, and do not include other key areas such as orientation (see Griffin 1970; Holland 2007; Holland et al. 2006; Wang et al. 2007), endocrine control (Berthold 1996; Wingfield et al. 1990), or biological rhythms (Berthold 1996; Gwinner 1990). Specifically, we 1st discuss mechanisms of fuel acquisition and storage and then discuss fuel utilization during flight. We also discuss some relatively unique features of bat migration (torpor and reproductive allocation) and summarize some key questions for future bat research.

FUELING THE JOURNEY

Fuel selection by birds for migration has been reviewed previously (Jenni and Jenni-Eiermann 1998). Energy metabolism can be fuelled by any 1 or a mixture of the 3 macronutrients (carbohydrate, protein, or fat), but it is clear that fat should be the fuel of choice for migratory flight. The cost of flight increases with body mass and consequently fuel sources with a high ratio of energy to mass should be favored. On a dry matter basis, lipids provide approximately twice the

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* Correspondent: lmcguir5@uwo.ca

energy of either carbohydrates or protein, and when coupled with the fact that lipids are stored nearly anhydrously, the difference increases to 8–10 times the amount of energy on a wet mass basis (Jenni and Jenni-Eiermann 1998; Ramenofsky 1990). Birds can fuel migratory flight almost exclusively with stored fat (Jenni and Jenni-Eiermann 1998; McWilliams et al. 2004), and often store large quantities of fat during migration seasons. Fat is stored in subcutaneous and abdominal fat depots and can account for >50% of total body mass (Berthold 1993; Piersma and Gill 1998). Migratory birds also may increase protein stores by growing larger lean body components (muscles and organs) to increase the functional capacity of flight and digestive machinery, and to provide amino acids required for the maintenance of citric acid cycle intermediates (anaplerotic flux), gluconeogenesis, water production, or a combination of these, during flight (Jenni and Jenni-Eiermann 1998; Lindström and Piersma 1993).

There is limited evidence that bats use fat as a primary fuel source during flight, and their fuel storage patterns during migration are essentially unknown. The most direct method to determine fuel selection is the respiratory quotient, the ratio of CO_2 produced to O_2 consumed (Frayn 1983; Walsberg and Wolf 1995). Bats are often difficult to train to fly in controlled conditions (e.g., a wind tunnel) and echolocating bats are particularly reluctant to wear a mask required to measure gas exchange. Nevertheless, a few estimates of respiratory quotient have been obtained. The respiratory quotient of the frugivores *Eidolon helvum* and *Hypsignathus monstrosus* indicated that fat provided 77–92% of the fuel during flight, and a decline in respiratory quotient with flight time suggests that at stable conditions in longer flights, fat may prove to be the exclusive fuel source following initial carbohydrate use (Carpenter 1986). Similar patterns of declining respiratory quotient with flight time were found for *Pteropus poliocephalus*, another frugivore (Carpenter 1985). The respiratory quotient for the carnivore–frugivore *Phyllostomus hastatus* in short flights (~1 min) indicated that carbohydrates were the sole fuel source (Thomas and Suthers 1972), in agreement with the hypothesis that carbohydrates provide the initial fuel. When fasted, the hovering flight of the nectarivore *Glossophaga soricina* is fueled mainly by stored fat (Welch et al. 2008) suggesting that fat would be the primary fuel during migratory endurance flights.

If bats do indeed fuel migration with lipids, fat stores should increase during migration. In practice this has been difficult to establish. There is some evidence for migration-related increases in fat stores by the insectivore *Tadarida brasiliensis* (O'Shea 1976). However, most species for which fat stores have been quantified during times of migration spend the winter in hibernation and consequently it is impossible to determine if the fat was accumulated to fuel migration or hibernation (e.g., Ewing et al. 1970; Kunz et al. 1998).

The quantity of stored fat is important, but so is the quality. Some birds appear to adjust the quality of fat stores during migration by increasing the proportion of unsaturated fatty acids (McWilliams et al. 2004). Unsaturated fatty acids are

mobilized more rapidly from adipocytes than are saturated fatty acids (Price et al. 2008), and may be preferentially oxidized by muscles (Leyton et al. 1987). Data about the variation in fatty acid composition in bats are limited. An evaluation of the prey items in fecal pellets suggested that bats prefer prey items high in unsaturated fatty acids (Schalk and Brigham 1995). Although no studies have investigated the fatty acid composition of adipose tissue in migrating bats, there are significant changes in the fatty acid profile of active and hibernating bats (Arévalo et al. 1990; Ewing et al. 1970).

There also are no data about variation in protein stores during bat migration. Studies of seasonal changes in body composition have been hindered by the elusive nature of many migratory bat species, and the fact that traditional methods of determining body composition require lethal sampling and lengthy chemical extraction processes. Recent advances in noninvasive measurement techniques for fat and lean mass, such as quantitative magnetic resonance analysis (L. P. McGuire and C. G. Guglielmo, pers. obs.) and dual-energy X-ray absorptiometry (Stevenson and van Tets 2008) may make it possible to determine fuel stores of migrant bats more easily.

Fuel Acquisition

To successfully complete a migratory movement, birds and bats must accumulate the energy and nutrients required to fuel the flight before departure. There are many physiological and behavioral adaptations that enable birds to rapidly deposit these nutrient stores and bats may potentially use similar mechanisms. In fact, the time and energy demands on bats may be even more severe. Many songbirds partition their time for different activities during migration by flying at night and resting and foraging during the day. In contrast, bats are not active during the day and must accomplish all foraging and migrating during the hours of darkness. This potential time limitation may enhance the selective pressure for efficiencies in any of the mechanisms described below, or perhaps bats have evolved an alternative mechanism to avoid the time constraint (see discussion of torpor).

Hyperphagia and diet selection.—Migratory birds deposit fuel stores quickly by entering a state of hyperphagia, with substantial increases in daily food intake (Bairlein 1990; Bairlein and Gwinner 1994; Berthold 1993; Blem 1990; Lindström 1991). Although there is very little research that suggests hyperphagia by bats in preparation for or during migration, 1 example is *T. brasiliensis*, which becomes hyperphagic before fall and spring migrations (Widmaier et al. 1996). Current efforts to identify potential migration stopover sites for bats may provide study locations where fueling rate can be measured using plasma metabolite analysis (McGuire et al. 2009, in press), or perhaps relative frequency of feeding buzzes.

In addition to eating more food, many bird species shift their dietary preferences (e.g., seeds, fruits, or invertebrates) to obtain the nutrients they require or to take advantage of

abundant resources (Bairlein and Gwinner 1994; McWilliams and Karasov 2005). Bats generally do not exhibit the same degree of dietary plasticity (e.g., an insectivorous bat will not eat berries). Therefore, the ability of bats to choose prey items based on physiologically relevant criteria (e.g., fat content) is probably limited. However, at least some species of insectivorous bats appear to prefer prey items high in unsaturated fatty acids during the summer (Schalk and Brigham 1995), suggesting the possibility of diet selection during periods of migration.

Seasonal variability in available food resources also may affect diet selection. Bats may simply consume whatever resources are available at the time. In the case of *Leptonycteris curasoae*, a nectarivorous migrant, the diet shifts from C3 plants in the winter to CAM plants during migration and the summer (Fleming et al. 1993). The change in nectar consumption appears to be driven by resource availability, rather than by active selection to enhance migration ability; *L. curasoae* migration follows the timing of CAM flowering species, suggesting that the bats migrate because of nectar availability, and not selecting specific nectars to fuel the migration. Similarly, it has been suggested that spring migration of hoary bats (*Lasiurus cinereus*) is timed to coincide with seasonal irruptions of moths in New Mexico (Valdez and Cryan 2009).

In an interesting twist, some bat species may actually take advantage of migration by other species. *T. brasiliensis* feeds opportunistically on migrating moths (Lee and McCracken 2005) and in Europe, *Nyctalus lasiopterus* feeds on migrating songbirds (Ibáñez et al. 2001; Popa-Lisseanu et al. 2007).

Digestive system flexibility.—The digestive system (alimentary tract, liver, and pancreas) exhibits remarkable variation in size and functional capacity in migratory birds (McWilliams and Karasov 2005). Hypertrophy is a generalized response of the digestive system to hyperphagia, which increases the demand to process food (Dykstra and Karasov 1992; McWilliams and Karasov 2001, 2005). Some birds that fly in short bouts and stop to refuel frequently along their migratory journey dramatically increase the size of digestive tract organs on a seasonal basis (Guglielmo and Williams 2003). On the other hand, species that make long-distance nonstop flights across inhospitable landscapes may reduce the size of the digestive system just before departure to minimize mass and metabolic cost during periods of flight; the so called ''guts don't fly'' hypothesis (McWilliams and Karasov 2005; Piersma 1998; Piersma and Gill 1998; Piersma et al. 1999). Furthermore, the breakdown of protein for fuel in flight appears to be preferentially directed at the gut, resulting in the ''shrinking gut'' phenomenon, which, according to the gut limitation hypothesis (McWilliams and Karasov 2001), can impair refueling capacity after arrival (Karasov and Pinshow 2000; Klaassen and Biebach 1994; Lee et al. 2002; McWilliams and Karasov 2001). All of these processes combined can mean that birds arrive after a long flight to a stopover with relatively small and impaired digestive systems,

increase them dramatically during peak refueling, and then reduce them again just before departure (Piersma et al. 1999).

We predict that bats will generally maintain enlarged digestive systems during migration seasons and probably not decrease them before flight in most circumstances. With few diurnal records of migrating bats, we assume that bats migrate during overnight flights, stopping each morning. If bats refuel each night, then increasing the size of nutritional organs should be favored, minimizing the time required for refueling and increasing the time available for migrating. Preliminary evidence suggests that bats do feed nightly. Analysis of stomach contents of *L. cinereus* and *Lasionycteris noctivagans* killed at wind turbines during migration revealed that 96% had fed that night (J. Reimer and R. M. R. Barclay, University of Calgary, pers. comm.).

Hepatic lipid synthesis capacity.—Elevated food intake and rapid fat deposition place elevated demands on the liver for postabsorptive processing of nutrients. Although some of the fat deposited in fat depots originates directly from the diet, fat also can be synthesized de novo in the liver from carbohydrate and protein precursors. Thus, it may be expected that the biochemical pathways of lipid synthesis may be up-regulated during the migration season. Fatty acid synthase is a hepatic enzyme that uses the substrates malonyl-coenzyme A (malonyl-CoA) and acetyl-CoA to produce the 16-carbon saturated fatty acid palmitic acid (Smith 1994), which can be further extended and desaturated by other enzymes known as fatty acid elongases and desaturases (Jakobsson et al. 2006). During the migration of western sandpipers (*Calidris mauri*) liver fatty acid synthase activity increases by about 2-fold (Egeler et al. 2000) and the mass of the liver doubles (Guglielmo and Williams 2003), resulting in greatly elevated lipid synthesis capacity. Similar changes occurred in Δ-9-desaturase activity, suggesting that increased desaturation capacity also is important during the migration season (Egeler et al. 2000).

The natural diets of insectivorous bats can be high in lipids, and therefore enhanced lipid biosynthetic capacity may not be required during migration. Stomach contents of *T. brasiliensis* during pregnancy and lactation averaged 60% lipids on a dry matter basis (Kunz et al. 1995). However, direct measurements of the diets and hepatic biosynthetic capacity of bats are required to assess the generality of this pattern.

Torpor and body temperature reduction.—In birds, approximately two-thirds of the total energy cost of migration is incurred during stopover, where energy expenditure is strongly linked to thermoregulatory costs (Hedenström and Alerstam 1997; Wikelski et al. 2003). In cooler weather, a significant amount of the metabolic fuel acquired during feeding may be oxidized to maintain body temperature, and is therefore not available to be stored for later use during migratory flight. Hummingbirds appear to use torpor at night during stopover refueling, saving fat acquired during foraging to be used during migratory flight and not in overnight thermoregulation (Carpenter and Hixon 1988; Hiebert 1993). Many birds do not have the ability to use torpor (McKechnie and Lovegrove

2002), yet some appear to lower their body temperature during the migration period, potentially to enhance their ability to deposit and store fuel (Butler and Woakes 2001).

Temperate bats are well known for their ability to enter daily torpor, and for some, long periods of uninterrupted hibernation (Davis 1970; Lyman 1970; Speakman and Thomas 2003). Many bats need to deposit fuel stores before hibernation at a time when temperature and prey availability are both declining. One strategy used by these bats is bouts of daily torpor, which minimize daily energy expenditure and enable greater nutrient storage for less foraging effort (McGuire et al. 2009; Speakman and Rowland 1999). Therefore, it is possible that migrating bats could minimize energetic costs during the inactive periods by entering torpor and saving their fuel stores for flight. During spring migration, male hoary bats (*L. cinereus*) readily entered torpor when placed in a cooled environment (Cryan and Wolf 2003).

The ability of bats to use torpor may prove to be a critical difference between birds and bats during migration. For birds, migration is very energetically costly and consequently there are a large number of potential adaptations made to adjust to those energy demands. However, if bats are able to use torpor to substantially reduce the energetic costs of migration, many of the adaptations observed in birds relating to hyperphagia and digestive system function may not be needed by bats.

FUEL UTILIZATION DURING FLIGHT

In flight, birds and bats alike must maintain very high rates of energy expenditure (approximately 10–15 times basal metabolism—Speakman and Thomas 2003; Winter and von Helverson 1998), and thus they must be able to mobilize, transport, and oxidize metabolic fuels quickly enough to meet energy demand. Classic exercise models developed using data for running mammals predict that exercise as intense as flight should be fueled almost completely by carbohydrate oxidation with fat oxidation contributing <20% of the energy (Roberts et al. 1996). Of the fat used by running mammals, most comes from intramuscular lipids, with only 25–50% delivered from adipose stores by the blood (Weber et al. 1996). Consequently, at high exercise intensities, only 5–10% of energetic requirement for a typical nonvolant mammal is supplied from stored fat. In stark contrast to this fuel selection pattern, birds fuel migratory flight almost exclusively with fat, yet the biochemical and physiological mechanisms that make this possible are very poorly understood (Guglielmo et al. 2002; McWilliams et al. 2004; Weber 1988).

Fatty acid transport proteins.—The main factor apparently responsible for the limited use of extramuscular lipids in exercising nonvolant mammals is restricted transport across muscle membranes (Vock et al. 1996; Weber 1988). To achieve high rates of extramuscular fat oxidation, migratory birds substantially up-regulate fatty acid transport proteins in flight muscles (Guglielmo et al. 1998, 2002; McFarlan et al. 2009). Plasma membrane fatty acid binding protein (FABPpm) and fatty acid translocase (FAT/CD36) are muscle membrane

proteins responsible for up to 80% of the transfer of fatty acids across muscle membranes (Luiken et al. 1997, 1999). They are strongly up-regulated during migration in white-throated sparrows (*Zonotrichia albicollis*—McFarlan et al. 2009). Heart-type fatty acid binding protein (H-FABP) is a cytosolic protein required to receive incoming fatty acids and transport them to be oxidized in mitochondria. H-FABP is one of the most abundant cytosolic proteins in the flight muscles of migratory birds and is seasonally up-regulated during migration (Guglielmo et al. 2002; McFarlan et al. 2009).

Despite the phylogenetic constraints of their mammalian ancestry, bats may have converged on a similar solution to birds to overcome limitations on the use of extramuscular fat to fuel flight. We are currently testing this hypothesis by studying seasonal changes in the expression of FABPpm, FAT/CD36, and H-FABP in migrating and nonmigrating *L. cinereus*. Encouraging data come from *Myotis lucifugus*, which is known to up-regulate H-FABP expression during hibernation (Eddy and Storey 2004), a physiological challenge that also requires high dependence on extramuscular fat stores.

Muscle oxidative capacity.—Bird flight muscles must have a high oxidative capacity to support the intense aerobic exercise required to fly, and this capacity may increase during migration to meet the high demands for fat oxidation. As a result, bird flight muscles have small-diameter muscle fibers, which increase surface area for oxygen and fuel transport, and a high proportion of fast oxidative glycolytic fibers (George and Berger 1966). Fiber diameter also is smaller in long-distance migrants compared to short-distance migrants and sedentary species (Lundgren and Kiessling 1988). Similarly for bats, comparisons of muscle in a migratory species (*T. brasiliensis*) and a nonmigratory species (*Artibeus jamaicensis*) suggest that migrants are better adapted for periods of sustained flight (Foehring and Hermanson 1984; Hermanson and Foehring 1988). To confirm that the differences are related to migration rather than due to foraging strategy or some other factor, more comparisons of migratory and nonmigratory species are necessary.

Mitochondrial volume density, as well as activities of key oxidative enzymes (e.g., citrate synthase, cytochrome oxidase, 3-hydroxy-acyl-CoA-dehydrogenase, and carnitine palmitoyl transferase) of bird flight muscles are typically high, and may become elevated during migration (Driedzic et al. 1993; Evans et al. 1992; Guglielmo et al. 2002; Lundgren and Kiessling 1985; Marsh 1981). Migrant bats are predicted to exhibit similar characteristics.

The activities of oxidative enzymes in bat pectoralis muscle are among the highest reported for vertebrate muscle and the relative capacities of lipid- and carbohydrate-specific enzymes suggest that lipids are the primary fuel for flight (Armstrong et al. 1977; Yacoe et al. 1982). Furthermore, insectivorous bats depend more on fat than do frugivorous species, which use more glucose due to their increased dietary glucose (Yacoe et al. 1982). Although there are no data about migration-related changes in oxidative capacity in bats, oxidative capacity decreases during hibernation when energy demand is low

TABLE 1.—Research questions to be addressed in future studies of bat migration physiology.

Fuel acquisition
- What is the size and composition of fuel stores?
- Do fat stores become more unsaturated?
- Do bats enter a state of hyperphagia during fuelling?
- Do bats store lean mass and how is it allocated between flight and digestive machinery?
- How flexible is the gut?
- How do liver size and metabolism change?
- What is the role of torpor in fuel acquisition?
- How do bats refuel during migration (stopover duration, refueling rate)?

Fuel utilization
- What is the fuel mixture used during flight?
- Do migrating bats use food ingested preflight or feed on the wing?
- Can bats maintain endurance flight using extramuscular fat stores?
- How abundant are muscle fatty acid transporters and are they seasonally modulated?
- Does muscle aerobic capacity increase during migration (enzymes, capillarity, and mitochondrial volume density)?

Reproductive allocation
- What are the trade-offs in energetic demand for migration and reproduction?
- How do spring and fall migration differ due to reproductive activities?
- What sex-based variations in migration physiology result from reproductive behaviors?

(Armstrong et al. 1977). During migration, bats should increase the already high oxidative capacity of pectoralis muscle to compensate for the increased energy demands of migratory flight.

TRADE-OFFS BETWEEN MIGRATION AND REPRODUCTION

For most of the factors we have described, we predict the selection pressures imposed by vertebrate flight will result in convergent evolutionary responses by bats and birds. In many ways, migration by bats and birds may be similar; however, the reproductive strategy of some bat species may make interpretations of physiological stress and energetic demands difficult. Temperate migratory birds travel from winter to summer grounds where they breed and rear young before returning to the wintering grounds. The demands of migration and reproduction are separated in time. For some bats, mating occurs (at least partially) during fall migration and females store the sperm over winter, becoming pregnant during spring migration (e.g., Cryan 2008; Kunz 1982; Shump and Shump 1982a, 1982b). The temporal overlap of migration and reproduction has physiological consequences resulting from competing time and energy demands. Adaptations or behaviors favoring migration may conflict with reproduction or vice versa.

An example of the conflict between migration and reproduction is the effect of sex on use of torpor during the spring migration of *L. cinereus*. At lower ambient temperatures, males readily enter torpor in response to cold challenge, whereas pregnant females increase metabolic rate to maintain normothermic body temperature (Cryan and Wolf 2003). The use of torpor enables males to save energy and potentially to wait out unfavorable migration conditions with little energetic cost. At the same time, females incur greater energetic cost and are forced to remain active during conditions when they would otherwise enter torpor. Further studies of bat migration physiology are likely to identify other situations of conflict between the demands of migration and reproduction.

CONCLUSIONS

We have identified several areas where we predict that the selective pressures of vertebrate flight have resulted in convergence between birds and bats. The proposed common features of migration provide a starting point for generating testable predictions about the physiology, biochemistry, and energetics of bat migration. We propose a list of key research questions that should be addressed in the study of fuel acquisition and utilization by migratory bats (Table 1). Understanding the similarities and differences between bat and bird migration will lead to insights about the evolution of migration and flight.

To keep our review concise, we have only considered simplified, stereotypical models of migration. However, in many cases bat migration is anything but simple. Many species have differential migration, with females moving farther than males (Cryan 2003; Fleming and Eby 2003), potentially placing stronger pressure for physiological specialization on females. First-year bats may continue somatic growth during fall migration, and thus greater physiological stress on 1st-year bats could cause age-biased mortality, as suggested by Tuttle and Stevenson (1977). Some species also appear to be partial migrants, where not all individuals or populations migrate (e.g., *T. brasiliensis*—Fleming and Eby 2003), presenting valuable opportunities for comparative studies. These factors are important to consider when planning studies of migratory species.

Bat migration, and particularly migration physiology, is a field that is only beginning to receive the research attention that is needed. With much to learn, our objective was to present a summary of our knowledge about basic bird

migration physiology and, where available, any data about bat migration. We hope this provides incentive for readers to address some of the questions that we have identified.

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Special Feature Editor was R. Mark Brigham.